ORNITHOPTERA EUPHORION (GRAY) (LEPIDOPTERA: PAPILIONIDAE): SPECIES OR SUBSPECIES?

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Abstract

On available evidence, Ornithoptera euphorion (Gray) is considered to be the sister-species of O. richmondia (Gray), not a subspecies of O. priamus (Linnaeus) unless both taxa (plus O. croesus Wallace) are included. A suggestion that a sister-taxon relationship exists between Ornithoptera Boisduval and Madagascan Pharmacophagus Haase, rather than Troides Hübner, is rejected. Trogonoptera Rippon is maintained as a distinct genus.

Introduction

For many years the polytypic Ornithoptera priamus (Linnaeus) was the only species of birdwing butterfly recognised in Australia. More recently (e.g. Common and Waterhouse 1981) the southernmost population, O. richmondia (Gray), has been accepted as distinct, although Haugum and Low (1978-79) had argued cogently against this. Hancock (1983, 1991) considered that both O. richmondia and O. euphorion (Gray) warranted specific rank, based on their sister-species relationship. Removing O. richmondia but retaining O. euphorion in O. priamus made the latter species paraphyletic. Hancock (1991) also noted that both these species appeared to be more closely related to O. croesus Wallace than to O. priamus.

In a recent study of *Ornithoptera* Boisduval, Parsons (1996a, b) included *O. aesacus* (Ney), *O. croesus* and *O. euphorion* as subspecies of *O. priamus*, without adequate explanation and despite the fact that none conforms to his definition of the latter as expressed in his tables. He continued to regard *O. richmondia*, which differs only in two weak characters (first instar larval and pupal colour, which are frequently intraspecifically polymorphic in swallowtails), as distinct. That arrangement has been followed by Braby *et al.* (1997) in their recent review of common names.

That arrangement is untenable. Below, we provide a discussion of characters, including several overlooked or misinterpreted by Parsons (1996a, b), that, in total, demonstrate a sister-species relationship between *O. euphorion* and *O. richmondia*. Parsons (1996a, b) also suggested that the Madagascan genus *Pharmacophagus* Haase, not *Troides* Hübner, was the sister-taxon to *Ornithoptera*. This, too, is discussed below.

Characters

Male genitalia. Haugum and Low (1978-79) noted that, whilst the male harpe of *O. euphorion* is similar to that of *O. priamus* and different from the shortened harpe of *O. richmondia*, the valvae are closer to *O. richmondia* than *O. priamus* in shape, particularly with regard to the protruding marginal-apical bulge and shape of the cavity of the valva. The shortened harpe, often

used as a defining character for *O. richmondia*, is seen also in *O. croesus* and is relatively short also in typical *O. p. priamus*. Haugum and Low (1978-79) noted that the differences in the harpe between *O. richmondia* and *O. euphorion* or *O. priamus* are no greater than those between *O. croesus* and *O. c. lydius* Felder or between *O. priamus* subspecies such as *O. p. priamus* and *O. p. caelestis* (Rothschild).

Male thorax. The patch of red lateral hairs below the wing base is reduced in both *O. euphorion* and *O. richmondia.* In *O. priamus* these red areas are more extensive.

Male abdomen. The abdomen has extensive black lateral shading in both O. euphorion and O. richmondia; this is also evident in O. croesus. In O. priamus the abdomen is primarily yellow without these blackened areas.

Male wing shape. Both the forewing and crenulate border of the hindwing are more rounded in O. euphorion and O. richmondia than in O. priamus.

Male wing pattern. The irridescent submarginal-posterior band on the forewing is consistently reduced and the cell veins on the hindwing underside are more extensively blackened in O. euphorion, O. richmondia and O. croesus than in O. priamus.

Female thorax. The patch of red hairs below the wing base is reduced and extensive red areas are present on the pronotum and mesonotum in both *O. euphorion* and *O. richmondia*, unlike the condition seen in *O. priamus* (Haugum and Low 1978-79). *O. croesus* has extensive lateral red areas (as does *O. priamus*) and small red markings on the pronotum and mesonotum. *O. aesacus* has the thorax wholly black.

Female abdomen. The abdomen is extensively blackened dorsally and laterally in both *O. euphorion* and *O. richmondia*; some blackening is also present in *O. croesus.* It is pale or only weakly darkened in *O. priamus* and all other *Ornithoptera* species (*O. chimaera* (Rothschild) and *O. rothschildi* Kenrick are pale with broad black rings).

Female wing pattern. There are strong similarities in the wing patterns of O. euphorion, O. richmondia and O. croesus, distinguishing them from O. priamus. Of particular note are the large submarginal hindwing spots and grey-suffused hindwing pale areas, tending yellowish-grey submarginally.

Mature larva. The pale saddle on abdominal segment 4 is absent in both O. euphorion and O. richmondia. Both species also have most of the tubercles black with a pale (reddish or whitish) medial band. In both O. croesus and O. priamus the pale saddle is present and most of the tubercles are reddish or pale with only the tips black.

Pupa. The green (rather than yellowish-brown) pupa and pupal diapause (Sands *et al.* 1997) are specialisations of *O. richmondia*. The yellowish-brown pupa and lack of diapause are widespread plesiomorphies.

Discussion

Given the allopatric nature of the taxa involved, O. croesus, O. euphorion and O. richmondia cannot be shown with certainty to be specifically distinct from O. priamus. Hybridisation studies to date are inconclusive and have not been properly documented; hence they should not be used to determine specific status. However, given the long acceptance of O. croesus as a valid species, plus the current acceptance of O. richmondia as distinct, there appears no option but to treat O. euphorion in a similar manner.

We know of no grounds for considering *O. aesacus* as anything other than a separate species; the male wing colour and genitalia are distinctive and resemble those of *O. alexandrae* (Rothschild). We recommend the continual recognition of *O. euphorion* at the species level, as the sister-taxon to *O. richmondia*. This arrangement is supported by presumably synapomorphic characters of the abdomen, thorax and mature larva. The common name 'Cairns Birdwing' may continue to be applied to it, with 'New Guinea Birdwing' retained for *O. priamus*. Two of the three apomorphic characters used to separate *O. richmondia* from *O. priamus* by Parsons (1996a, b: colour of larval tubercles and loss of abdominal saddle) also apply to *O. euphorion* (the third character being the green pupa); thus even by Parsons' own analysis *O. euphorion* cannot be included within *O. priamus*.

Parsons (1996a, b) placed Ornithoptera as the sister-genus to Madagascan Pharmacophagus (regarded by him as monotypic) and his phylogenetic and biogeographic reconstruction relies heavily on this assumption. That placement rests solely on pupal morphology and is contrary to all previous arrangements, which associate Ornithoptera with Troides and Trogonoptera Rippon. The lateral ridge-like protuberance on abdominal segment 4 of the pupa, well developed in Atrophaneura Reakirt (including Pachliopta Reakirt), is also present, on a reduced scale, in Pharmacophagus antenor (Drury). It is not evident in Ornithoptera or any other genus in the Troidini. This and the suite of characters noted by Hancock (1988), covering male and female genitalia (notably the elongate bursa copulatrix), great reduction of hindwing androconia (scent-organ) and larval morphology, clearly align the Madagascan Atrophaneura (Pharmacophagus) antenor with the Indian A. (P.) hector (Linnaeus). Larvae of both species feed on Aristolochia: A. antenor on Ar. acuminata and A. hector on Ar. indica. The relationship between Atrophaneura and its subgenera Pharmacophagus and Pachliopta is supported by the monomorphic pupal colour plus the presence of extensive red areas on the abdomen (Parsons 1996a), the latter seen elsewhere only in Cressida Swainson.

Pupae are strongly selected for crypsis, hence the small differences observed between *Ornithoptera* and *Troides* pupae are probably not particularly significant. We see no grounds for considering these two genera (or subgenera, depending on individual preference), as anything other than sister-taxa. Nor do we accept the placement of *Trogonoptera* as a subgenus of *Troides* by Parsons (1996a), based almost entirely on early stage characters. The relationship of *Trogonoptera*, *Troides* and *Ornithoptera* is supported by the shape of the female bursa copulatrix, similar variations in pupal colour and the absence of red wing scales (Parsons 1996a). The unribbed ovum glue (Parsons 1996a), presence of golden-yellow wing areas, abdominal colour, shape of the juxta and harpe (Hancock 1991) and the form of the sterigma (Orr 1988) further support the sister-taxon relationship between *Troides* and *Ornithoptera*, as does the occurrence of natural hybrids (Sands and Sawyer 1977). The ovum glue is weakly ribbed in *Trogonoptera* and strongly ribbed in other troidine genera (Parsons 1996a).

Tyler *et al.* (1994) found that computer-derived cladograms using early stage characters differed widely from those using adult characters. A cladogram using all available characters ('total evidence' *sensu* Tyler *et al.* 1994, Parsons 1996a, b and, in all but name, Hancock 1983, 1988) produced another alternative. Clearly not all of them can be correct and any phylogenetic reconstruction based on such analysis should be interpreted cautiously; this appears to be particularly the case with early stage characters.

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